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BOTANICAL GAZETTE

SEPTEMBER 1907

THE STRUCTURE AND RELATIONSHIPS OF THE POTAMOGETONACEAE AND ALLIED FAMILIES¹

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(WITH PLATES XIV-XVIII)

In the alluring search for primitive monocotyledons which shall throw light on the vexed question of the origin of the group, the Helobiae have received much attention, including as they do such a wide range of forms, reaching from great simplicity to considerable complexity. It is generally agreed that those monocotyledons which possess a stocky rhizome or bulb have reached a degree of specialization which renders them less favorable for a study of primitive features than are the forms which have a more elongated axis showing distinct nodes and internodes. The Potamogetonaceae are prevalently of the latter class, and the genus *Potamogeton* has been considered by SCHENCK (27) and others to represent a number of stages in the evolution of aquatic monocotyledons from ancestors which inhabited marshy ground. It has been more than once suggested that the monocotyledons have been derived from dicotyledonous ancestors through adaptation to an amphibious mode of life, so that the genus *Potamogeton* deserves study from all standpoints. A quite different view of the origin of monocotyledons has been proposed by CAMPBELL (3), who seeks to link the group with heterosporous Filicineae, especially Isoetaceae, through such forms as *Naias*.

It is proposed in the present paper to discuss certain features of the structure of *Potamogeton* which have apparently been overlooked,

¹ Contributions from the Phanerogamic Laboratories of Harvard University, No. 9.

but which seem to be significant from the standpoint of phylogeny; also to bring together the salient points concerning the structure of the other genera of the family, so that if possible their relationships may be worked out. A few genera belonging to allied families have been included in the account.

I wish here to record my obligations to the following, who have very kindly supplied me with material: Professors G. F. ATKINSON and W. W. ROWLEE and Mr. H. H. SMITH, of Cornell University, Mr. H. H. BARTLETT of the Gray Herbarium, Mr. J. G. HALL of the North Carolina Experiment Station, Mr. A. JEFFREY of Toronto, Dr. R. G. LEAVITT and Mr. A. A. EATON of the Ames Botanical Laboratory, Mr. C. P. SMITH of Carmel Bay, Cal., and especially to Professor M. L. FERNALD of the Gray Herbarium, who has been kind enough to determine most of the species employed in the research.

Potamogetonaceae

In this family the following genera have been accessible for study from preserved material: *Potamogeton* (thirteen species), *Ruppia*, *Zostera*, *Phyllospadix*, *Cymodocea*, *Zannichellia*. Celloidin was found to be the most favorable imbedding material for all except the smallest forms, for which paraffin was used. Serial sections through the nodes and other critical regions were in all cases studied.

POTAMOGETON

THE LEAFY SHOOT.—The mode of origin of this member has been carefully worked out by IRMISCH (12), who distinguishes between main shoots and reserve shoots. The internal structure of the upper internodes of such shoots varies somewhat widely in the different species, and upon the basis of the characteristics as revealed by a cross-section, together with the leaf structure, RAUNKIAER (21) has proposed a classification of the species and devised a convenient key. The differences between the species consist in the presence or absence of cortical bundles, and in the degree of union of the strands which compose the vascular part of the central cylinder. *Fig. 11* shows at low magnification the structures occurring slightly above one of the upper nodes of the leafy shoots. At the upper side of the figure is the section of the petiole with its median and lateral traces. Below this

are the two fused stipules, sheathing the stem; their main bundles are barely visible at this magnification, but are situated at the angular swellings. Between the stipules and the stem is an axillary bud. The stem shows the lacunar cortex characteristic of aquatics, and a well-developed central cylinder. *Fig. 13* shows certain of these features more clearly, and also makes visible the numerous cortical strands which lie in the angles of the meshes.

Since the course of the leaf traces furnishes a key to the structure of the internodal stele, it is proposed to describe the course of the bundles in a well-developed species, *P. natans*. Stated briefly, the seven or more leaf traces shown in *fig. 11* fuse to form three, which enter the central cylinder, pass down through one internode separately at the periphery of the central cylinder (see DEBARY 7, p. 270.), then approach one another, pass down through a second internode in the form of what may be styled a "trio" of bundles, and at the third node become indistinguishable on account of union with the bundles of the central cylinder. Since the leaves are arranged alternately in two vertical rows, there are two groups of leaf trace bundles in the cross-section of any internode. This is illustrated in *fig. 14*, which will be rendered clear by the following diagram (*fig. 1*), in which t_1 , T_1 , t_1 represent the traces of the next higher leaf, t_2 , T_2 , t_2 those of the second higher leaf, while the remaining bundles are those which are styled by DEBARY cauline, since they do not lead directly to any leaf. Although the petiole contains seven or more bundles, as shown in *fig. 11*, they enter the central cylinder as three, since the lateral bundles on each side fuse with one another. On each side this fusion bundle is joined also by the median bundle of the stipule of that side. An anastomosing branch may be sent to the median leaf trace. The bundles at the base of the petiole, like those of the internode, are devoid of xylem, but a lacuna represents the absent vessels, and shows that the bundle is collateral. As the bundle enters the cortex of the stem, ringed vessels or tracheids make their appearance, and the bundle becomes somewhat swollen and almost amphivasal, owing to increase in the number of tracheids which come more and more nearly

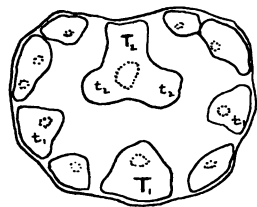


FIG. 1

to surround the phloem, thus recalling the condition found by the writer in grasses (6), where, however, the appearance is more pronounced. With the three foliar traces groups of mechanical fibers enter the central cylinder. After anastomosing with other bundles present at the node, the three lose their xylem and proceed downward at the periphery of the stele, occupying the middle region of three contiguous sides of the roughly oblong section of the stele (*fig. 14*). At the next node they enlarge, move toward the center of the stele, and the xylem again appears, first at the inner side of each bundle, filling the cavity, thence spreading around the phloem, so far as to render the bundle almost or quite amphivasal (*fig. 15*); the two lateral ones anastomose with other bundles, then the three approach, including between them an island of parenchyma which is surrounded by the xylem of the bundles. The xylem again disappears, as does also the island of parenchyma, which is replaced by a cavity which persists through the succeeding internode. Thus the "trio" is formed and descends to the next node, where tracheids appear once more, first around the cavity, and thence spreading around the bundles until the two lateral ones become amphivasal. At the same time the three bundles enlarge, the two lateral ones fuse, then separate, and all three join other bundles of the nodal complex, such as those of the axillary branch which enters at this level. Both the petiole and the fused stipules contain many small bundles consisting of fibers or of thin-walled cells or of both. These bundles descend into the cortex of the stem, some of them fusing with similar bundles of that region derived from petioles and stipules of higher leaves. In this way apparently arise the very numerous cortical strands characteristic of this species, and it may be stated in general that those species which possess a cortical system derive it from the petioles and stipules. Two points in the foregoing account seem worthy of emphasis, namely, the presence of amphivasal bundles wherever the leaf trace bundles are about to fuse with other bundles, and the very different course pursued by the leaf traces from that which is seen in most monocotyledons.

Concerning the insertion of branches it should be noted that the phloem of the bundles shows a remarkable enlargement just before joining the stele of the main stem, as is shown in *fig. 12*. The elements

of the phloem at this point are narrow cells with very thin walls, quite unlike the well-marked sieve tubes which are seen in other parts of the stem. Such bundles are frequently seen to be amphivasal just before they are inserted on bundles of the main stele. Species with an axial cylinder like *P. natans* are: *P. perfoliatus*, *P. Nuttallii*, *P. praelongus*, etc..

P. natans has been chosen for the foregoing description, not because it presents the most primitive structure of any of the species, but because the vascular tissues are well developed, probably on account of the transpiration from the numerous and large floating leaves. What seems to be a more primitive disposition of the vascular bundles of the central cylinder is seen in *P. pulcher* (fig. 19), also a form with some floating leaves, but with broad submerged leaves instead of the phyllodes of *P. natans*. The course of the leaf trace bundles in *P. pulcher* resembles that already described, with the noticeable difference that the three bundles do not unite to form a "trio," but merely approach one another in the medulla of the second internode after the insertion of the leaf, giving the appearance shown in cross-section (fig. 20). A diagram (fig. 2) will make clear the topography of the central cylinder: as before, t_1 , T_1 , t_1 represent the traces of the next higher leaf; t_2 , T_2 , t_2 those of the second higher leaf; while the remaining bundles are cauline. As in the former species, amphivasal bundles occur at the nodes when two bundles are about to fuse. In spite of the liberal size of the leaves, and the fact that some of them float, no cortical bundles are present in the stem (fig. 19). Numerous small bundles are present in the stipules, but they turn abruptly inward and enter the central cylinder, while the median bundle of each stipule as usual joins the lateral leaf trace.

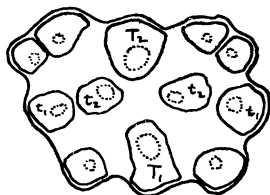


FIG 2

The two species already considered represent two types of central cylinder found in the genus. They are evidently closely related, and the *natans* type may evidently be regarded as derived from the *pulcher* type by the partial fusion of the three leaf traces during their descent through the central cylinder. At least two other types may be distinguished, in one of which the bundles of the central cylinder have

further fused so as to form three more or less clearly separated areas, as is shown in the photograph of *P. crispus* (fig. 28) and in fig. 3. T_1 , t_2 , T_2 , t_2 of the preceding diagrams have united to form the central area, while the remaining bundles form the lateral regions. T_1 may be distinguished from T_2 by the double lacuna of the central area. As usual, three (or sometimes five) leaf trace bundles enter the central cylinder, the large median one joining the central area, and the laterals, each composed as usual of bundles from the petiole and one from the stipule of that side,

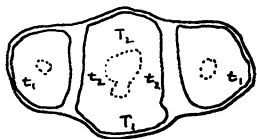


FIG. 3

join the lateral areas of the central cylinder. DEBARY (7, p. 274) gives a singularly misleading description and inaccurate diagrams of this species, owing probably to the crudity of his methods of investigation. SCHENCK (28, p. 41) has given a correct interpretation of the appearances presented by a cross-section, and I have confirmed his statements by series of sections through the nodes. *P. crispus* is no more an "anomalous monocotyledon" (DEBARY) than are the other species of *Potamogeton*, since, as shown above, its vascular system can be easily derived from that of *P. pulcher*.

A further reduction or fusion of the vascular elements is shown in the species of which *P. pectinatus* (fig. 18) may be taken as the type. In the internodes the xylem is represented only by a central cavity surrounded by parenchyma and phloem, but at the nodes a division of the stele into three areas is more or less plain. The last fact suggests that the condition found in this species has been derived from that seen in *P. crispus*, since ancestral characters are apt to persist at the nodes.

The behavior of the small bundles derived from the petiole and stipules shows great variation in the different species. (1) They may descend into the cortex of the succeeding internode, constituting the usually numerous cortical bundles of a number of species, e. g., *P. natans*, eventually joining others of the same kind, or finding their way into the central cylinder at a lower node. (2) They may descend a short distance into the cortex, then disappear, while a short distance below the node other strands make their appearance in the cortex, to disappear before the next node is reached, e. g., *P. Robbinsii*.

(3) They may (with the exception of the central bundle of each stipule, which joins a lateral leaf trace) disappear soon after entering the cortex, leaving the stem without cortical bundles, e. g., *P. crispus*. (4) They may enter the central cylinder immediately, like the leaf traces, leaving the stem devoid of cortical bundles, e. g., *P. pulcher*. To this should be added the peculiar case of *P. Nuttallii* (fig. 5), in the upper leaves of which the median bundle of each stipule fuses with the neighboring lateral leaf trace bundle, and from the fusion is given off a strand which descends into the cortex. The cortical bundles of this species are not numerous (six to eight), and form a complex anastomosis with the central cylinder at the level of the lower part of the node. In general it may be stated that when a species possesses cortical bundles they are derived from the small bundles of the petiole and stipules. This view is confirmed by the fact that such bundles are universally present in the petioles and stipules, even when they are absent from the stem. As to composition, the cortical bundles range from complete collateral bundles to mere groups of a few fibers, and moreover the character of a bundle may change greatly in its course, being composed mostly or altogether of phloem at one level and only of fibers at a slightly different level. SCHENCK (28, pp. 48, 54) is of the opinion, and my observations confirm his view, that all these strands represent real fibrovascular bundles, which share in the reduction shown by the vascular tissues of the central cylinder.

The extent to which mechanical tissue is present is, according to SCHWENDENER (30), dependent on whether the plant grows in still or in running water. But different species occupying a similar habitat may differ widely in respect to the presence of mechanical tissues; for example, *P. natans* is abundantly provided with cortical strands, while *P. pulcher* entirely lacks them, yet both are inhabitants of ponds, and both possess floating leaves. Judging from over forty species for which data are available, there is no relation between the presence of cortical bundles and a totally submersed or a partly floating habit. Neither can a relation be established between size of leaf or stem and presence or absence of cortical bundles. That these strands are not primitive structures, but have arisen in connection with the mechanical necessities of the leaves and stipules is indicated by three facts. (1) In the creeping stem, which has rudimentary sheathing leaves devoid

of stipules, the small cortical strands are few and wanting, even in species which possess them abundantly in the leafy shoot. (2) As will be pointed out later, in *P. natans*, *P. Nuttallii*, etc., the cortical strands spread upward into the peduncle, but fuse with the strands of the vascular ring (see below) or fade away soon after reaching the fertile part of the axis. (3) As stated above, small bundles are of constant occurrence in the petioles and stipules, even if the stem is free from them.

THE CREEPING STEM.—According to IRMISCH (12), this does not represent the main stem, but certain lateral members of the extensively branched system. The structure differs in several noteworthy respects from that of the leafy stem. The central cylinder is flattened in accordance with the dorsiventral nature of the stem, as is seen in the photograph of *P. pulcher* (fig. 21), and presents a truly dicotyledonous looking ring of collateral bundles (fig. 22), though the appearance is somewhat masked by the large size of a dorsal and a ventral bundle. These two bundles may meet in the center of the stele in case the stem is much flattened. All of these are cauline strands, whose disposition is practically unaffected by the entrance of the insignificant leaf traces from the thin deciduous scale leaves. Hence there is no “trio” of bundles, and the disturbing elements are branches, not leaves. Considering a node lacking a branch, the large dorsal and ventral bundles are seen in a series of sections to pass through the node sometimes without anastomosis with other bundles; they swerve slightly toward the middle of the stele, while the lateral bundles partly close the gaps thus left in the vascular ring, and give off roots on all sides of the stele. In case a branch is present at a node, the dorsal and ventral bundles not merely approach the center of the stele but become much enlarged owing to excessive development of phloem (fig. 17), and fuse to form a large amphivasal strand which then breaks up into several amphivasal bundles. These anastomose with peripheral bundles of the stele and with the bundles of the branch which enter at this point. The bundles at the base of the branch likewise show a greatly swollen phloem, which is a conspicuous feature in the figure. It will be recalled that owing to the distichous arrangement of the leaves, the ascending stem shows two bundles on opposite sides of the central cylinder, which bundles are the median traces of the two next higher

leaves. In the creeping stem, however, the two opposite bundles are seen from the foregoing to be connected with the origin of branches. As in the leafy shoot, vessels are present only at the nodes, and are represented by a cavity elsewhere. The endodermis is plain, of U-form, and suberised. *Fig. 16*, representing the creeping stem of *P. natans*, which should be compared with *fig. 13*, shows another point of difference between the creeping and the leafy stem. While cortical bundles are abundant in the latter, they are much scarcer or absent in the former, owing apparently to poor development of leaves and the absence of stipules. In case cortical bundles are absent in the leafy shoot, they are lacking also in the creeping stem, as may be seen from the figures of *P. pulcher*. In accordance with the sheathing character of the reduced leaves, the leaf traces enter the central cylinder separately, as may be well seen in *P. perfoliatus* or *P. heterophyllus*, which have better developed basal leaves than has *P. pulcher*.

THE FLORAL AXIS.—SCHENCK (28) and others have not failed to notice that the peduncle has a different disposition of bundles from that in the leafy shoot, but the earlier observers have apparently overlooked the regularity in the arrangement of the bundles. *Fig. 23* shows the appearance of a section through the fertile part of the floral axis of *P. natans*. The arrangement is evidently circular, and the bundles are collateral. Branches leading to the flowers do not have a gap above their point of exit, but spring from one bundle or from two adjoining bundles. Well-developed tracheary tissue is present in all of the bundles, in marked contrast to the condition seen in an internode of the vegetative axis. *Fig. 24* represents an appearance which occasionally occurs; here the bundles constitute a nearly closed vascular tube. The circular arrangement of bundles occurs in every species which I have examined, even in such slender forms as *P. hybridus*, the peduncle of which shows four separate strands, each surrounded by an endodermis (*fig. 26*). The basal part of the axis shows the same arrangement as that represented in the figures, but the strands are apt to be more widely separated. Cortical strands are also present in the peduncle of species such as *natans*, which show many such strands in the leafy stem (*fig. 25*); they either join bundles of the circle or dwindle away shortly after reaching the fertile part of the axis. A ring of collateral bundles in the floral axis of Eleo-

charis is figured by PLOWMAN (19), and is stated by him to be characteristic of the Cyperaceae. A similar condition is found in *Triglochin* (see below). The resemblance of these axes to the stems of dicotyledons can hardly fail to be noticed, and I am inclined to attach phylogenetic importance to the feature, rather than explain it on physiological grounds, as is suggested by SCHENCK (28). The persistence of ancestral features in the reproductive axis has been pointed out by SOLMS-LAUBACH (31) and by SCOTT (29), and the status of this as a general principle has of late received strong confirmation, especially from the work of JEFFREY, who in his memoir on the Abietineae (14) sums up the evidence in favor of the principle. In *Potamogeton* we seem to have another case in point, for the peduncle shows the primitive dicotyledonous arrangement of bundles, which moreover are collateral throughout their course.

GENERAL.—The affinities of the genus *Potamogeton* may best be discussed later, but we may here consider the relations of the species. The main question at issue is as to whether the species with large floating leaves or those with small submersed leaves are primitive, or whether, as RAUNKIAER (21) believes, the species with large submersed leaves are to be so regarded. One criterion for the decision of the question is the structure of the central cylinder in the various species. In his admirable memoir on submersed plants SCHENCK (28) has described and figured the central cylinder of a series of species, starting with *P. perfoliatus*, in which the bundles of the internodal stele are separate, and ending with *P. pectinatus*, in which the stele consists of thin-walled cells surrounding a central cavity, and he concludes that the series represents a process of fusion and reduction of the vascular tissues. In another work (27) the same author expresses the view that the pondweeds have sprung from terrestrial plants which passed through the amphibious, then the swimming, and finally the submersed stage: "*P. natans* würde nach dieser Ansicht die ursprünglichste Form unter den heutigen Arten noch vorstellen." With the general principle of reduction here stated the present writer is in accord, but it seems to him that the place of honor should be awarded to some such species as *P. pulcher* for the following reasons: (1) *P. natans* has some of its submersed leaves specialized as phyllodes, while in *P. pulcher* the submersed leaves are broad and differ from

the floating ones mainly in their thinness; (2) It is probable that the separate bundles in the central cylinder of *P. pulcher* represent a more primitive condition than the "trio" of *P. natans*. There seems to be every reason to believe that the small-leaved submersed forms with a stem showing a concentric stele are to be regarded as simplified by reduction. Further, the group of species with stipules adnate to the petiole represented by *P. filiformis*, *P. pectinatus*, and *P. Robbinsii* are probably quite specialized forms, since they are connected with such forms as *P. natans* by a small group including *P. spirillus* and *P. hybridus*, in which the stipules are slightly adnate and the spikes are of two kinds, the emersed ones cylindrical, and the submersed ones capitate, consisting of four to six flowers. It should also be noted that *P. Robbinsii*, etc., have their flowers in an interrupted spike.

RUPPIA MARITIMA

This monotypic form has been uniformly placed in the same family as Potamogeton on account of its emersed inflorescence, perfect flowers, and alternate leaves. The complex arrangement of branches characteristic of Potamogeton is here represented by a creeping axis giving off roots and leafy shoots, as described by IRMISCH (12). The structure of the stem is comparatively simple: inside a lacunar cortex is a central cylinder of the type of *P. pectinatus*, viz., with a central cavity surrounded by small thin-walled cells. Tracheids are present at the nodes. Each leaf possesses a central bundle and two very slender lateral ones. The central bundle enters the central cylinder directly, as in Potamogeton; while the lateral bundles descend into the cortex of the stem for a greater or less distance, though they do not reach the next lower node, but dwindle away and disappear, as is illustrated in the diagram, fig. 9. This condition has in all probability been derived by reduction from that in which the cortical bundles joined the central cylinder at the next node below the insertion of the leaf to which they belong, for it is unreasonable to suppose that the leaf traces should originally have had no connection with the main conducting channels of the stem. Thus the cortical bundles of Ruppia belong to VAN TIEGHEM's second group (32, p. 751). The course of these bundles, and the occurrence of xylem at the nodes, as well as the filiform leaves and submergence of all parts

of the plants except the flowers, leads to the view that *Ruppia* is an example of simplicity by reduction.

POSIDONIA

MAGNUS has given a short account of the stem structure of *P. oceanica* (17). According to his description, the conducting tissue of the central cylinder is flanked by a mass of mechanical fibers, and the cortex contains numerous small bundles of fibers and also a few conducting bundles. No account is given of the course of the leaf traces, and material has not been obtainable so far for the present research.

ZOSTERA

The widely distributed species *Z. marina* has been the subject of frequent study. EICHLER (10) described the sympodium of floral axes, and SAUVAGEAU (23) has given the best account of the vegetative structures of the five species, referring to the older literature on the subject. The creeping stem is monopodial, and bears the long ribbon-shaped alternate leaves, while the ascending branches are sympodes bearing the flattened spadices. In all these regions the main structural features are the same, namely, a wide, somewhat lacunar cortex containing two vascular strands and inclosing a narrow central cylinder. The structure of the last, however, differs considerably in the various regions of the plant. *Fig. 29*, from the lower part of the ascending shoot, shows the simplest condition, with a central lacuna and four masses of phloem, therefore representing four fused bundles. This condition is present also in the apical parts of the creeping stem, and arises from the distichous arrangement of the leaves. The older parts of the creeping stem show four additional bundles in the stele, alternating with the first-formed bundles. Xylem fills the lacuna at the nodal regions, but is nowhere well developed. From the sheathing base of a leaf a median bundle enters the central cylinder directly; while on each side two or more lateral traces fuse and join the cortical bundle on its side, which at the same level sends a branch to the central cylinder, as shown in the diagram, *fig. 6*. From the leaf also enter a large number of small bundles of fibers which run down in the outer region of the cortex; in the creeping stem these may be thin walled

or even absent. The peduncle shows a structure similar to that of the stem figured; no circle of separate bundles such as in *Potamogeton* is found, but the central cylinder consists of two united bundles.

The well-defined cortical system of this plant is a characteristic feature which at once separates the genus from *Potamogeton*. In *P. Nuttallii*, however, we have a suggestion as to how the condition in *Zostera* may have arisen, as described above (p. 167); the lateral bundle entering the stem from the petiole and stipule may give off a branch which descends through the cortex. The chief difference between this condition and that in *Zostera* is that in the latter genus the cortical strand is continuous up and down through a number of internodes. Whether a leaf trace at once penetrates into the central cylinder, or descends at the periphery of the cylinder, or descends altogether outside the cylinder, appears to be a feature readily modifiable in the monocotyledons, as has been pointed out by the writer (6), and in almost every family of monocotyledons there are members in which at least some of the leaf traces pursue a cortical course for the length of an internode before joining the central cylinder. Apparently this condition is derived from that in which all bundles of the leaf trace join the stele directly.

According to SAUVAGEAU (23), *Z. Muelleri* and *Z. tasmanica* show two to five cortical bundles on each side in place of the single one of *Z. marina*. These bundles anastomose with one another at the node, and send a branch to the central cylinder, while receiving a single bundle from the leaf, i. e., the leaf has a median and only two lateral traces.

The affinities of this genus are by no means clear. Like *Potamogeton* it has an elongated inflorescence which here reaches a high degree of specialization. The totally immersed habit of the plant, together with the hydrophilous mode of pollination by means of filamentous pollen also indicate specialization. The vascular structures may have been derived from the condition found in *Potamogeton*, as is suggested above, but the resemblance is not striking, especially when we consider the eight radially arranged bundles of the central cylinder. The process of evolution has apparently separated *Zostera* far from its relatives.

PHYLLOSPADIX

This Pacific coast genus, nearly related to *Zostera*, has been inadequately studied, though DUDLEY (8, 9) gives a good general account, and corrects several mistakes of earlier writers, e. g., the supposedly tuberous habit of the base of the stem as erroneously figured in ENGLER and PRANTL (11). Through the kindness of Mr. C. P. SMITH, I have been able to study alcoholic material of *P. Scouleri* from Carmel Bay, California. As DUDLEY points out, the basal part of the stem, far from being tuberous, is an elongated rhizome, along which the leaves are arranged alternately right and left. In general plan, the structure of the stem resembles that of *Zostera marina*, showing a comparatively small central cylinder and two slender cortical bundles. To the latter the lateral leaf trace bundles are attached, while the median trace joins the central cylinder directly. These statements apply equally to the ascending stem, represented in fig. 30, which shows certain features more clearly on account of the absence of roots. As may be seen in the figure, two lateral traces enter the stem on each side of the median trace, and attach themselves to one of the cortical strands which then sends in a branch to the central cylinder. Thus the disposal of the leaf traces differs no more from that in *Zostera marina* than does this from other species of *Zostera*. The central cylinder is in most respects similar to that of *Zostera*, showing four bundles in a section through an internode of the ascending stem. In the upper part of such a stem the bundle derived from the median trace of a leaf runs somewhat apart from the other bundles of the central cylinder, and in general the vascular strands of this genus show a tendency to be more widely separated than in *Zostera*. The floral axis does not show the ring of bundles seen in *Potamogeton*, but these are arranged in a tubular stele, and there are two cortical strands as in the lower part of the stem. These features of the floral axis are in accord with its specialized character in this species. Numerous mechanical strands enter the stem from the leaves, especially in the ascending part of the stem, but they are not numerous nor thick walled in the creeping stem. As in *Zostera* the pollen is filamentous. The anatomical characters afford no reason for questioning the conclusion of DUDLEY, that the genus is derived from *Zostera*.

CYMODOCEA

This genus shows several points of resemblance to *Zostereae*, e. g., the filamentous pollen, elongated creeping stem, frequently ribbon-shaped leaves, and, as will be seen, its vascular structure is closely related. The best general account is that by BORNET (2) of the species *C. nodosa*, though the account of the vascular anatomy is meager. SAUVAGEAU has described certain features of the stem and leaf structure of a number of species (24). The only species accessible to me has been *C. manatorum*, and to it the following account applies. The internodal stem (fig. 31) shows a differentiation in its cortex which is characteristic of the genus. An outer zone free from lacunae contains near its inner limit a broken circle of cortical bundles, and surrounds an inner zone which is lacunar. The circle of bundles really consists of two sets, an arc-shaped group of four or five on each side of the central cylinder, which is somewhat flattened. Each of these groups corresponds to one of the two cortical strands of *Zostera marina*, and to the two to four strands of *Z. Muelleri* and *Z. tasmanica*. They are, as would be expected from analogy, connected with the lateral traces of the leaf, while the median leaf trace enters the central cylinder directly. At the node the cortical bundles of each side anastomose and send a branch which joins the central cylinder at the point of entrance of the median trace. Certain of these features are shown in fig. 32. As SAUVAGEAU figures for *C. serrulata*, the central cylinder consists of two bundles lying in the line which passes through the base of the leaf (fig. 31); the phloem contains several large sieve tubes, and the xylem of the two bundles is fused and is represented by a central lacuna. As the node is approached, tracheary tissue fills the lacuna, and at the point of entrance of the leaf trace that bundle of the stele lying toward the trace becomes amphivasal, quickly followed by the other bundle. After the entrance of the two bundles from the cortical system three amphivasal bundles are present in the stele, soon becoming two and changing to the collateral form as their xylem disappears and is replaced by the central lacuna. The cortical system of *Cymodocea* seems to be an extension of the plan seen in *Zostera marina*, *Z. Muelleri* forming an easy transition. The genus is to be regarded as a specialized one, judging from the anatomy and the filamentous pollen.

HALODULE

I have not examined material of this genus, but SAUVAGEAU'S account of the stem structure (24) leaves little doubt that it is derived from *Cymodocea* or one of its near ancestors. Instead of the arc of similar cortical bundles on each side of the central cylinder, *Halodule* shows one larger strand and a variable number of rudimentary strands forming an arc—apparently a more differentiated condition than that found in *Cymodocea*.

ZANNICHELLIA PALUSTRIS

The external morphology bears a general resemblance to that of *Potamogeton*, and the minor differences are stated in detail in IRMISCH'S classic work already referred to (12). The structure of the creeping and ascending stems is very similar, and carries the reduction observed in *Ruppia* a step farther. As stated by CAMPBELL (3) and confirmed by my observations, the central cylinder of the stem consists of thin-walled tissue inclosed in a distinct endodermis and surrounding a central cavity. The lacunar cortex lacks the two strands seen in *Ruppia*, for in *Zannichellia* the leaf contains a single trace which enters the central cylinder directly. Spiral tracheids are present at the nodes to nearly the same extent as in *Ruppia*, and are much more abundant than in *Naias flexilis* or *N. marina*. CAMPBELL makes the interesting observation that the filament of the stamen is traversed by tracheary tissue, showing in section usually two tracheids. The plant is totally submersed, and pollination is effected under water, a fact which points to a high degree of specialization. The single stamen and monoecious habit point in the same direction; in fact specialization and reduction are so great that the affinities of this monotypic genus are very uncertain.

Naiadaceae

NAIAS

On account of the simplicity and the exceptional development of its floral parts this genus has attracted much attention. Originally counted as belonging to *Potamogeton*, the tendency now is to put the genus in a family by itself. MAGNUS (15, 16, 18) has thrown much light on the morphology, and in his paper of 1870 gives an excellent

account of the earlier work. CAMPBELL (3) has studied *N. flexilis* by the aid of modern technique, and RENDLE (22) has recently revised the genus from the systematic standpoint. The last two mentioned authors summarize our knowledge of the morphology, so we may at once proceed to a discussion of the features which throw light on the affinities of the genus. My own observations have been confined to two species, *N. flexilis* and *N. marina*, obtained from several different localities with a view to confirming earlier accounts. The structure of the stem resembles that found in *Zannichellia*, and is figured for typical species by RENDLE; a cortex containing a circular row of lacunae incloses a slender stele which consists of thin-walled elongated cells surrounding a central lacuna. The endodermis is usually well marked. A single leaf trace enters the stele directly from each leaf. In *N. flexilis* a few ringed or spiral tracheids are to be seen at the nodes, especially the younger ones, also in the pedicel of the flower, and, according to CAMPBELL, in the young leaves as well. In *N. marina*, however, I am unable to find any trace of tracheary tissue, although this species is a stouter form than *N. flexilis*. The feature to which most significance has been attached is the simple flower, consisting either of a single ovule or single anther, inclosed in a "spathe." In early stages the micro- and megasporangiate structures are scarcely distinguishable, and CAMPBELL compares them with the sporangia of *Azolla*. This author argues for the derivation of the monocotyledons directly from pteridophytes, especially the Isoetaceae, through simply organized aquatics such as *Naias* or *Zannichellia*. According to this view the simplicity exhibited by the vegetative and reproductive structures is primitive. In marked contrast is the opinion of MAGNUS: "Bei *Naias* scheint mir vieles dafür zu sprechen, das wir es mit reducirter Einfachheit zu thun haben" (18, p. 222). It will be well to examine the evidence in some detail.

(1) On the view that *Naias* represents a reduced form derived from a land plant, the occurrence of tracheids at the nodes, in the pedicels of the flowers, and in the young leaves, receives ready explanation, for these regions are just the ones in which ancestral features are apt to persist. On the other hand, there seems to be no reason why a submersed aquatic which is primitively an aquatic should have any tracheids whatever. Under this head the evidence seems conclusive.

(2) "The flowers of *Naias* represent the simplest form which an angiospermous flower can assume, consisting simply of a single carpel with but one ovule, or of a single stamen which in most species has but one pollen cavity" (CAMPBELL 3, p. 12). The inaccuracy of the last statement can be easily shown. By sorting out the species described in RENDLE's paper, it is found that seven species have a unilocular anther, while twenty-three have the usual quadrilocular anther. Moreover, CAMPBELL figures a case where the anther of *N. flexilis* is partially divided by a partition. It would seem then that *N. flexilis* forms an exception to the condition obtaining in the genus, hence the similarity between megasporangiate and microsporangiate structures is not so great as supposed. Concerning the single stamen, it by no means follows that this necessarily indicates a primitive condition, for there are cases of monandrous flowers belonging to families which are admitted to be high in the scale, for instance Hippuridaceae and many orchids.

(3) The ovary of *N. marina* is surmounted by three stigmas (sometimes two), that of *N. microdon* by three stigmas, or by two stigmas and a spine-arm, or by intermediate conditions; other species show a varying number of stigmas (see RENDLE's figures). The number of stigmas in a flower is usually taken to indicate the number of carpels, e. g., some grasses have two stigmas though there is only one seed. In the case of *Naias*, EICHLER (10) is of the opinion that the evidence is untrustworthy, since the stigmatic branches are of relatively late appearance. It may be, however, that we have here a relic of the condition of the flower with several carpels.

(4) *Naias* has unisexual flowers, monoecious or dioecious; this is not regarded as being so primitive a condition as the hermaphrodite one exhibited by members of the Potamogetonaceae.

(5) Pollination in *Naias* is effected by means of the water in which the plants are immersed. This mode must be considered to be derived from the anemophilous mode, for non-motile spores in the higher plants are regularly carried through the air.

On the whole it seems to me that the claim of primitive simplicity for *Naias* cannot be maintained. The evidence goes to show that its structure is reduced in accordance with its aquatic habit. The genus stands very much isolated, but it has been suggested by MAGNUS that

its ovary might be derived from an ancestor of *Zannichellia* by the suppression of all the carpels but one.

Aponogetonaceae

APONOGETON FENESTRALIS

The creeping rhizome of this bizarre plant differs markedly from those found in Potamogetonaceae, being much less lacunar and having its cells loaded with starch. The vascular cylinder is poorly defined, since no endodermis is visible and the bundles are not numerous. Some of these lie at what is to be regarded as the periphery of the central cylinder, and a few others run in the medulla. Very few of these are amphivasal, and all are weak looking strands with their xylem hardly lignified. At intervals the peripheral bundles are connected by a girdle of vascular strands, so that an almost complete ring is formed. Seven or more traces enter from the sheathing base of each leaf, rapidly traversing the cortex and penetrating to near the middle of the stele, where they anastomose with one another and proceed downward through the medulla. Thus the vascular structure resembles that of the majority of monocotyledons which have a creeping rhizome much more than it does that of Potamogeton. In this respect and in its floral characters the genus seems more closely related to Alismaceae or Juncaginaceae than to the families so far discussed.

Juncaginaceae

TRIGLOCHIN MARITIMA

It is not intended to enter in any detail into the morphology of this genus, but to call attention to certain features which seem of theoretic interest. Contrary to the habit of the plants at the other end of the series, *Triglochin* has a stocky subterranean stem with short internodes, resembling *Acorus* and many of the sedges. *Fig. 33* shows its central cylinder; an endodermis is visible, within which are a number of bundles, mostly amphivasal, imbedded in fundamental tissue which is not lacunar as is the cortex, but contains much starch. In the center of the stele is an island of mechanical tissue. The presence of amphivasal bundles throughout the length of the stele easily distinguishes this genus from Potamogeton. The writer has already (6) expressed the view that such bundles arising in the nodes

by reason of fusion of leaf traces with other strands may continue in their amphivasal condition from one node to another in case the internodes are short, as is the case in a stocky stem such as occurs in this genus. The leaf traces are collateral and penetrate the cortex rather rapidly to enter the central cylinder. *Fig. 27* shows a transverse section through the floral axis. The exceedingly dicotyledonous looking ring of collateral bundles cannot fail to be remarked. Attention has already been called to the persistence of ancestral features in the floral axis. and we have here a particularly good case in point.

SCHEUCHZERIA PALUSTRIS

The rhizome of this monotypic genus bears a general resemblance to that of *Triglochin*, but its tissues are much more lacunar, both in the intra- and extra-stelar regions. The cortex lacks the mechanical fibers found in *Triglochin*, and the island of such tissue is absent from the stele. Numerous leaf traces enter the cortex from the sheathing leaves; the larger traces penetrate directly into the interior of the stele, while the smaller ones run down through the cortex for nearly the length of an internode before entering the central cylinder. The structure of the central cylinder of the rhizome is shown in *fig. 34*; leaf traces are to be seen in various stages of penetration in to the cylinder. Most of the bundles lie in a circle at the outer border of the stele, and it will be noticed that practically all of them are amphivasal, although CHATIN (4) figures them as collateral. It is probable that his figure is from a higher region of the stem, for I have found that in this region the bundles are more nearly collateral, i. e., with U-shaped xylem. It is of interest to add that in the upper nodes the leaf traces enter the stele through distinct gaps. The floral axis is strengthened by a thick fibrous ring, inside which are collateral bundles arranged in an irregular ring, with three or four lying a short distance farther in. Thus the arrangement is not so simple as in *Triglochin*.

The affinities of this and the preceding genus seem to be with Alismaceae rather than Potamogetonaceae, hence no attempt will be made at present to discuss this question.

Relationships

The view that the monocotyledons have been derived from the dicotyledons has been put on a new foundation by recent anatomical

studies. Since the correctness of this view is to be premised in the following discussion, it will be well to review the evidence for it. The two characteristic monocotyledonous features—scattered arrangement of the bundles and amphivasal form of bundle—are found not to occur in the seedling in families which have been examined in this respect (JEFFREY 13, CHRYSLER 5, PLOWMAN 19). On the contrary, the seedling shows a tubular stele with collateral bundles, such as is typical of a dicotyledon. Sooner or later some of the bundles turn into the medulla and show the amphivasal feature at some part of their course, eventually becoming leaf traces. These stages in ontogeny are believed to repeat stages in the phylogeny of the group. Occasional cases of apparent reversion to the primitive type occur in adult rhizomes, such as that of *Clintonia*. The tubular stele is found in the floral axis of some monocotyledons, and its occurrence here has been interpreted as the persistence of an ancestral feature. In this organ and in the leaves, moreover, only collateral bundles are found, which is the prevailing type in dicotyledons. A cambium, the lack of which was supposed to be a distinguishing feature of monocotyledons, has been demonstrated in *Gloriosa* by QUEVA (20), in the seedlings of a number of monocotyledons by ANDERSSON (1), in Cyperaceae by PLOWMAN (19), and most recently in the nodes of grasses by the present writer (6). It has been argued that in the last-mentioned case the cambium has persisted in regions where it is of use, and is therefore a vestigial not a rudimentary structure. As to geological evidence, many of the supposedly ancient monocotyledons have turned out to be gymnosperms, and there is no reason for believing that monocotyledons existed earlier than dicotyledons. Finally the researches of Miss SARGANT have shown how a monocotyledonous embryo may have been derived from a dicotyledonous one.

The present research has added to the evidence along at least one of the lines just mentioned. It has been shown that in *Triglochin* and various species of *Potamogeton* the floral axis contains a circle of collateral bundles, in which respect it is sharply distinguished from the leafy shoot, especially in *Triglochin*. It has also been pointed out that in the creeping stem of *Potamogeton*, where no large leaves send in traces, the central cylinder has a simple tubular form, though this appearance is often masked by the large size of the dorsal and

the ventral strand. In the elongated internodes of *Potamogeton* only collateral bundles occur, while in the shortened axis of *Triglochin*, to which many leaves are attached, amphivasal bundles are numerous. This apparently represents the direction of evolution. Lack of material has so far prevented me from studying the seedlings of any of the Helobiae, but the importance of such study is fully recognized, and cultures are in progress which it is hoped will shortly render it possible to fill this gap in the evidence.

Admitting then the derivation of the monocotyledons from dicotyledon-like ancestors, which of the genera studied most closely resemble the dicotyledons? There seems to be sufficient reason for considering *Potamogeton* the most primitive genus met with, as is indicated by the following facts:

(1) The stem of *Potamogeton* is not a shortened axis, such as is seen in many of the monocotyledons, e. g., the rhizome of *Triglochin*, which in all probability has been shortened and thickened in accordance with its geophilous habit.

(2) Xylem is well developed in the nodes, floral axis, and young stem of many species of *Potamogeton*. Its presence in these regions cannot be explained on physiological grounds, but must be regarded as the persistence of an ancestral feature. Conduction must be performed by the internodes as well as the nodes, therefore if the tracheary tissue were functional (i. e., rudimentary instead of vestigial) in the immersed species, its occurrence ought not to be localized.

(3) The separate strands present in the central cylinder of such species as *P. pulcher* are to be regarded as more primitive than the compound or fused cylinder seen in *Zostera*, etc.

(4) *Potamogeton* shows the circle of bundles in the floral axis more plainly than any other genus studied, with the exception of *Triglochin*. The significance of this feature has already been considered.

(5) The phloem in *Potamogeton* is particularly well developed, consisting of sieve tubes with evident sieve plates, and undoubted companion cells, though the latter are seldom so plain in monocotyledons as in dicotyledons.

(6) Some species of *Potamogeton* possess floating leaves. Though it is not denied that this may be a specialized feature, it has been well

argued by SCHENCK (27) that we have here a stage in the assumption of aquatic life by the genus. The leaves of all the other members of the family are submersed.

(7) The inflorescence is a spike or spadix, an admittedly primitive form. The other genera show a specialized spadix, such as *Zostera*, or a reduced inflorescence, as in *Zannichellia* (and *Naias*).

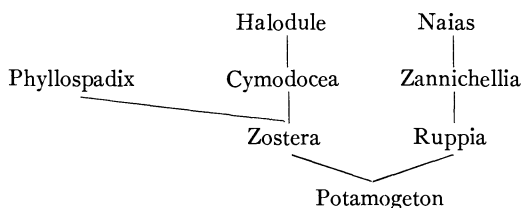
(8) The spadix in *Potamogeton* is raised above the surface of the water so that pollination is anemophilous. The nearest approach to this is in *Ruppia*, where the pollen floats on the surface of the water, while in the other genera the inflorescence is submersed and the pollen does not reach the surface. In connection with this habit the pollen of *Zostera* and *Cymodocea* is filamentous. Evidently these cases of hydrophilous pollination are adaptations.

(9) The floral parts are in whorls of four, which is a characteristic dicotyledonous number, although the whorls do not alternate in the simplest way. There is only slight coalescence of parts.

(10) The flowers are perfect, while in *Zannichellia* and *Naias* they are monoecious or dioecious.

As to the relationships among the genera, the tendency of recent classifications is indicated by the fact that the old family Naiadaceae is now split into four families, and one of these (the Potamogetonaceae) into five not very closely related sections. It appears that the leading principle at work in the evolution of the families has been that of simplification or reduction, both in the reproductive and the vegetative organs. Some features of specialization and complexity have also appeared, such as the filamentous pollen and flattened spadix of *Zostera*. This genus in spite of its peculiarities seems to stand more closely related to *Potamogeton* than to the reduced genera *Ruppia*, *Zannichellia*, and *Naias*, and its vascular system at least may be derived from that of *Potamogeton*, as has already been shown. The vascular system of *Ruppia* may represent a reduced condition derived from that of *Zostera* or *Potamogeton*, while *Zannichellia* and *Naias* are still more reduced both as regards the vascular system as a whole and the elements of which it is composed. *Naias* represents the extreme of reduction found in the group, for there is a single leaf trace, and tracheary tissue is found only in certain species, such as *N. flexilis*, and is confined to a few scattered tracheids at the nodes, the

pedicel of the flower, and the young leaves. In contrast to this simplification, the genus *Zostera* leads to a state of greater complexity in *Cymodocea* and *Halodule*, where the two cortical strands of *Z. marina* are replaced by two arc-shaped groups, each of several strands but with a similar relation to the leaf traces and central cylinder. *Phyllospadix* differs so little from *Zostera* in its vascular tissues, that if this were the only criterion both might be included in the same genus. *Triglochin* and *Scheuchzeria* appear to be only remotely related to the foregoing genera. Both are much more typical monocotyledons, as appears from the rhizome and flowers, and are more naturally related to the *Alismaceae*. *Aponogeton* seems to be more closely related to *Alismaceae* and *Juncaginaceae* than to *Potamogetonaceae*. The following diagram represents in a graphic way certain of the relations suggested in the foregoing account:



Summary

1. The course of the leaf traces in *Potamogeton* is not typically monocotyledonous, for in the more robust species the three traces run down through one internode at the periphery of the central cylinder before entering the medulla, where they descend through a second internode, finally fusing with cauline strands.

2. At the points of fusion the bundles are found to be amphivasal, while they are collateral throughout their internodal course.

3. The phloem of the bundles at the base of a branch shows a marked swelling.

4. The cortical bundles present in some species of *Potamogeton* are not regarded as a primitive feature, since they do not occur in the fertile part of the floral axis and occur only sparingly if at all in the creeping stem. They enter the stem as small strands from the stipules and petioles and are not as a rule connected with the principal leaf

traces. In *Zostera* and *Cymodocea*, however, there is a system of cortical bundles which are connected with all of the principal leaf traces except the median one.

5. The circle of collateral bundles found in the floral axis in *Potamogeton* and *Triglochin* is regarded as a relic of the ancestral dicotyledonous condition of the vascular system.

6. The evidence afforded by the vascular and floral structures indicates that *Potamogeton* is the most primitive genus of *Potamogetonaceae*. It shows more clearly than the other genera features characteristic of terrestrial life, though some of its species are apparently reduced forms.

7. Species of *Potamogeton* having both floating and submersed leaves and a central cylinder in which the bundles run separated from one another are regarded as the most primitive members of the genus. *P. pulcher* fulfils these requirements.

8. The other genera of *Potamogetonaceae* show further stages of reduction in accordance with their totally submersed habit. Their relationships are in some cases shown by the vascular structures.

9. In *Naiadaceae* the reduction is carried to such an extreme of simplicity that the affinities of the family are obscure.

10. *Aponogetonaceae* and *Juncaginaceae* are more typically monocotyledonous in their structure, and do not seem immediately related to *Potamogetonaceae*.

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EXPLANATION OF PLATES XIV–XVIII

PLATE XIV

Diagrams to show the course of the leaf traces in the different genera. In each diagram the upper part represents a transverse section through the node, and the lower part a longitudinal section through a node and part of the internode below it. The boundary of the central cylinder is indicated by broken lines, the median leaf trace by a double line, and the lateral leaf traces by single lines. In the vertical diagrams the median trace is represented for the sake of clearness as if entering from one side.

FIG. 4. *Potamogeton* (most species).—FIG. 5. *Potamogeton Nuttallii*.—FIG. 6. *Zostera marina*.—FIG. 7. *Phyllospadix Scouleri*.—FIG. 8. *Cymodocea manatorum*.—FIG. 9. *Ruppia maritima*.—FIG. 10. *Zannichellia* and *Naias*.

PLATE XV

FIG. 11. *Potamogeton natans*. Transverse section a little above an upper node of the leafy shoot, showing the petiole, fused stipules, axillary bud, and stem. $\times 15$.

FIG. 12. Same. Longitudinal section through an upper node, showing the swellings at the origin of leaf and branch bundles. $\times 20$.

FIG. 13. Same. Part of *fig. 11* more magnified; numerous cortical bundles are visible. $\times 20$.

FIG. 14. Same. Central cylinder of *fig. 13* more magnified. $\times 45$.

FIG. 15. Same. Transverse section through the central cylinder at a node of the leafy shoot. $\times 35$.

FIG. 16. Same. Transverse section through internode of the creeping stem; cortical bundles are absent. $\times 35$.

PLATE XVI

FIG. 17. *P. pulcher*. Transverse section through central cylinder of the creeping stem at the origin of a branch. $\times 20$.

FIG. 18. *P. pectinatus*. Transverse section through the leafy stem a short distance above a node. $\times 55$.

FIG. 19. *P. pulcher*. Transverse section through the leafy stem just above a node, showing the absence of cortical strands characteristic of this species. $\times 20$.

FIG. 20. Same. Central cylinder of *fig. 19* enlarged, showing the separated bundles. $\times 70$.

FIG. 21. Same. Transverse section through an internode of the creeping stem, showing the tubular central cylinder. $\times 20$.

FIG. 22. Same. Central cylinder of preceding figure. $\times 80$.

PLATE XVII

FIG. 23. *P. natans*. Transverse section through fertile part of the floral axis, showing a ring of bundles. $\times 35$.

FIG. 24. Same. Condition sometimes found in the floral axis. $\times 55$.

FIG. 25. Same. Section from near the base of the peduncle, showing cortical bundles outside the ring. $\times 20$.

FIG. 26. *P. hybridus*. Section through the floral axis. $\times 120$.

FIG. 27. *Triglochin maritima*. Transverse section through the floral axis, showing a ring of collateral bundles. $\times 25$.

FIG. 28. *P. crispus*. Transverse section through central cylinder. $\times 100$.

PLATE XVIII

FIG. 29. *Zostera marina*. Transverse section through an internode of the ascending stem. $\times 20$.

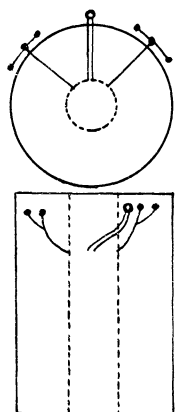
FIG. 30. *Phyllospadix Scouleri*. Transverse section through the ascending stem at the upper part of the insertion of a leaf. $\times 15$.

FIG. 31. *Cymodocea manatorum*. Transverse section through an internode of the stem. $\times 25$.

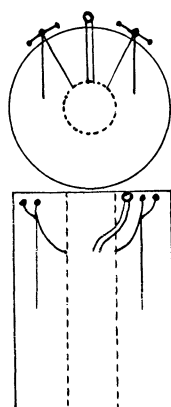
FIG. 32. Same. Transverse section through a node. $\times 30$.

FIG. 33. *Triglochin maritima*. Transverse section through the central cylinder of the rhizome. $\times 25$.

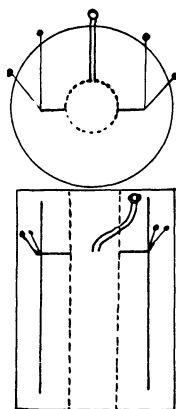
FIG. 34. *Scheuchzeria palustris*. Transverse section through central cylinder of the rhizome. $\times 30$.



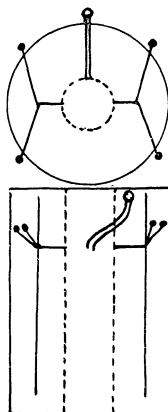
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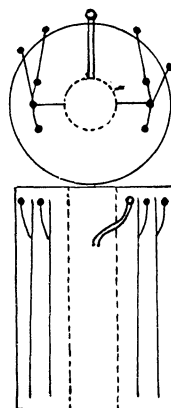
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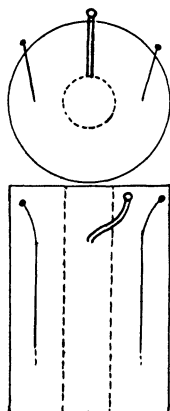
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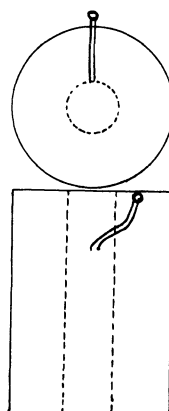
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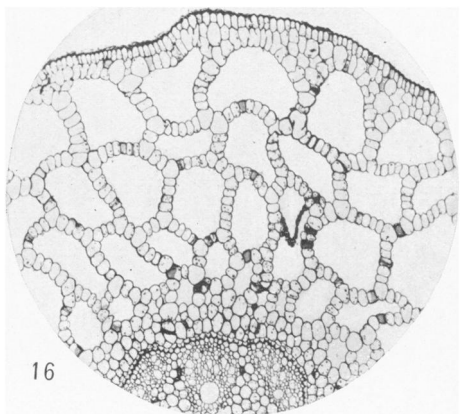
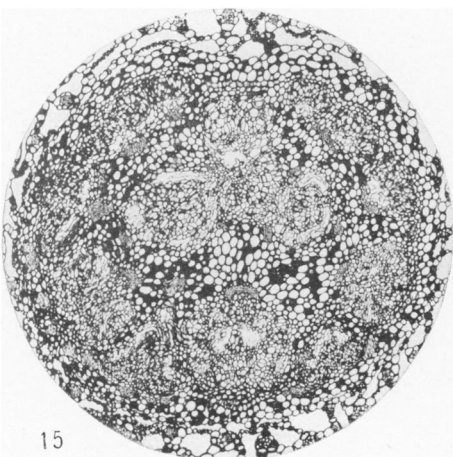
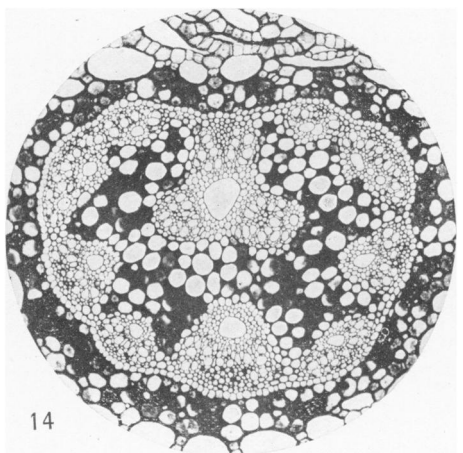
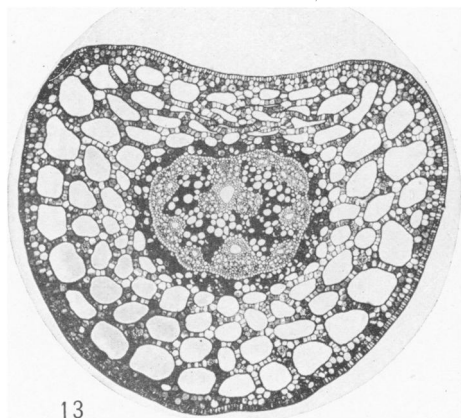
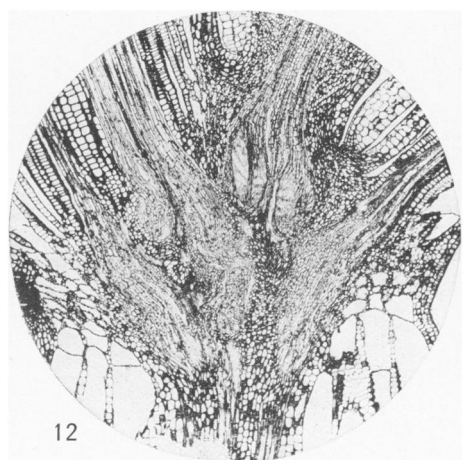
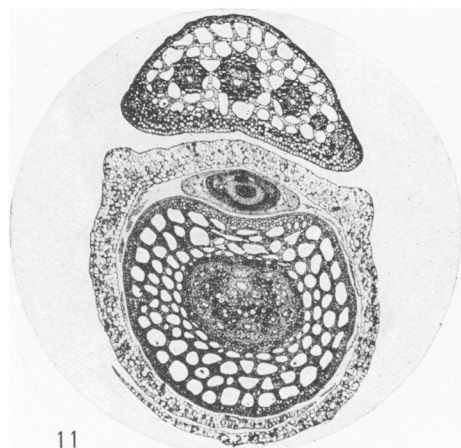
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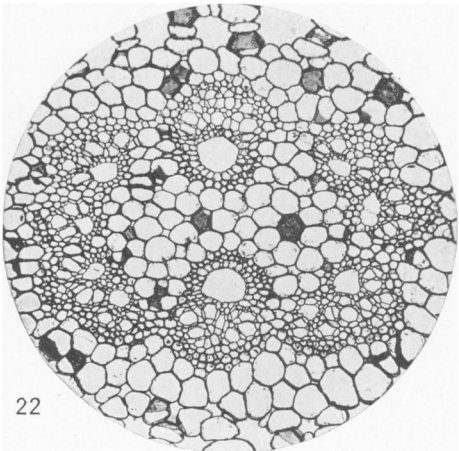
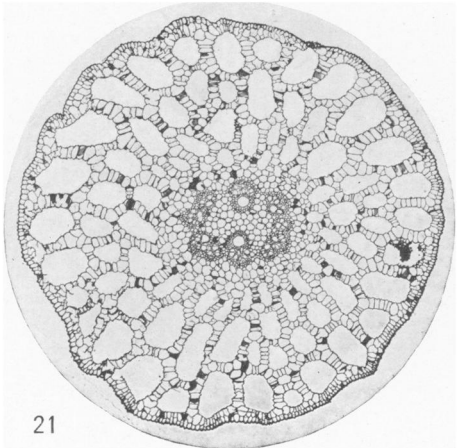
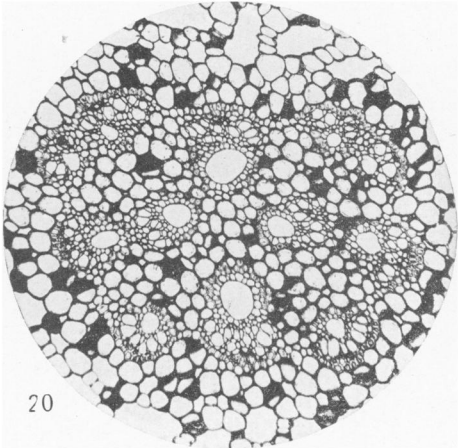
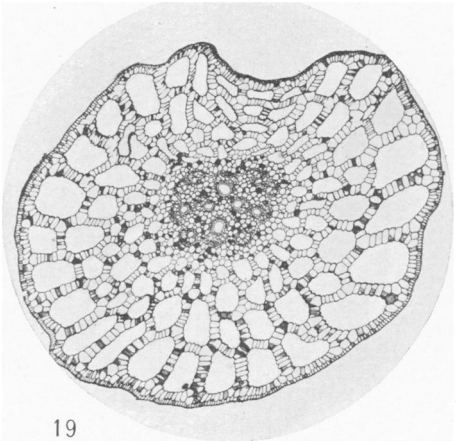
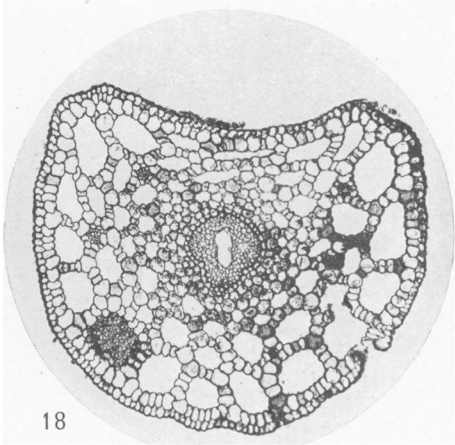
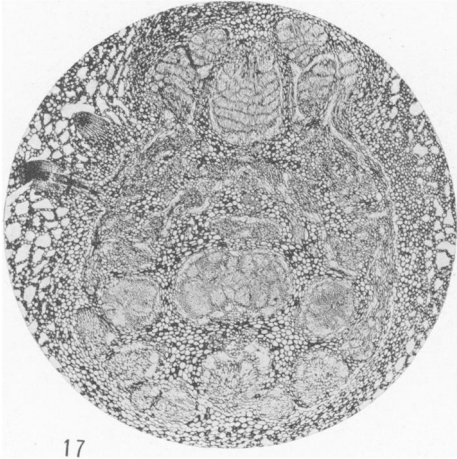


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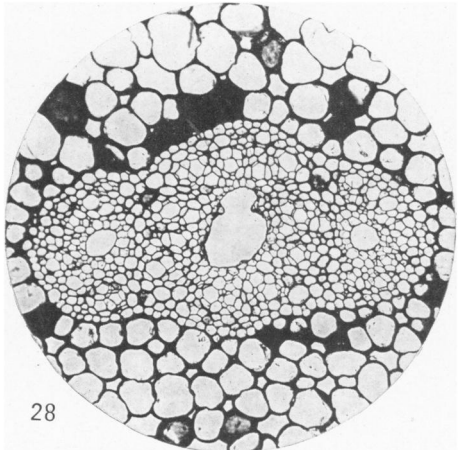
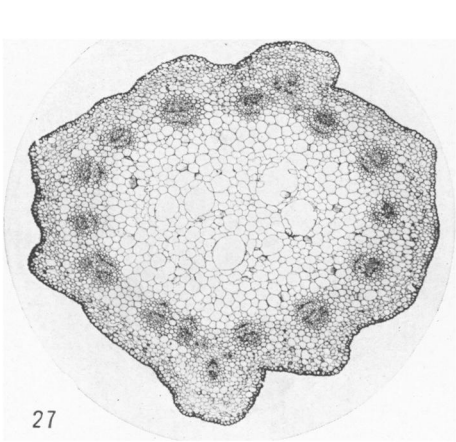
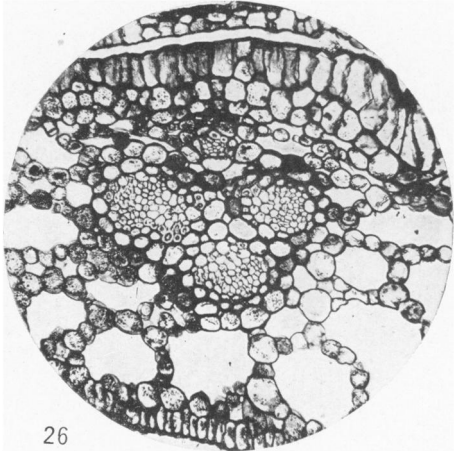
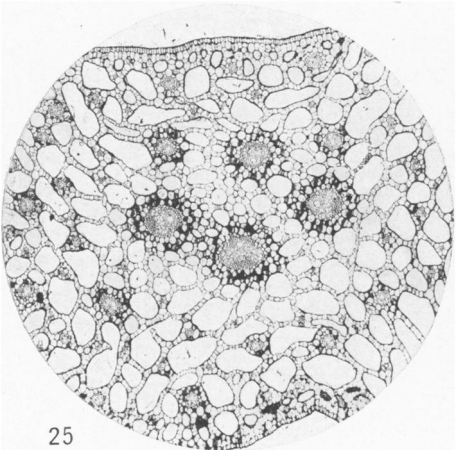
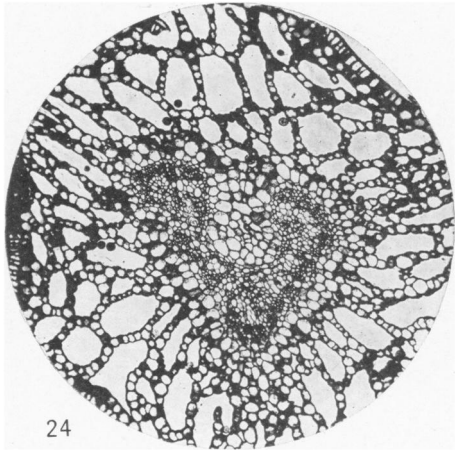
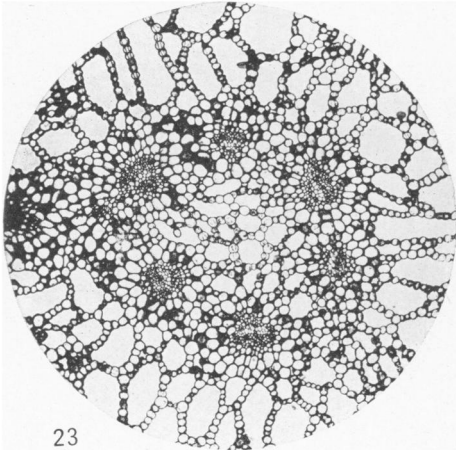
M. A. C. photo.

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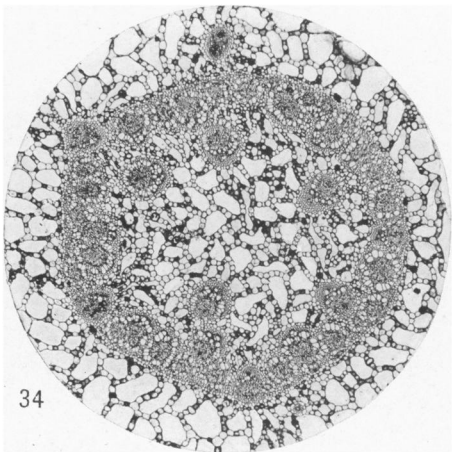
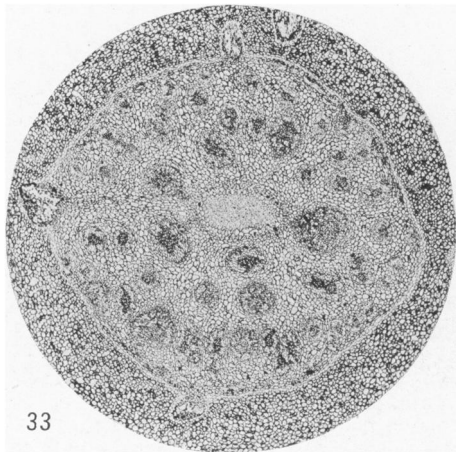
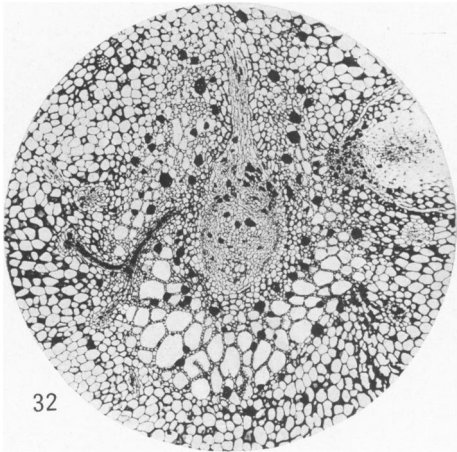
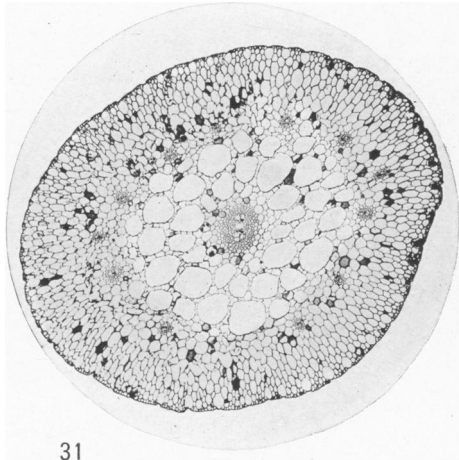
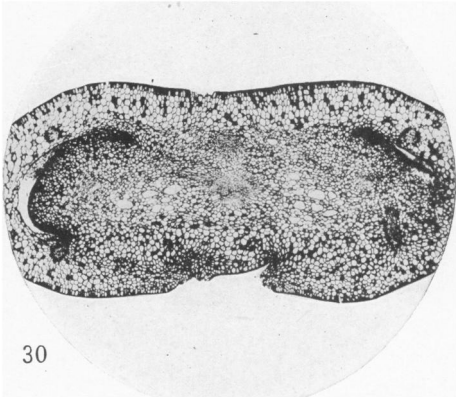
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